The impact of Alpine newts (*Triturus alpestris*) and minnows (*Phoxinus phoxinus*) on the microcrustacean communities of two high altitude karst lakes

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The zooplankton communities in two neighboring high altitude karst lakes of similar size and water chemistry were entirely different from each other. In one lake Alpine newts (*Triturus alpestris*) exploited the food resources during summer, in the other fish (European minnow, *Phoxinus phoxinus*) were the top predators. The zooplankton community in the fishless lake consisted of several big species of crustaceans, whereas rotifers dominated in the other. Although the diet of the newts consisted mainly of crustaceans, their predation pressure was low compared to that of the fish population. Population size of adult newts was at least ten times smaller than that of sexually mature fish (1570 newts versus 17420 minnows).

INTRODUCTION

The shift in a zooplankton community from big crustaceans towards smaller species due to size selective predation of fish was first described by HRBÁČEK (1962) and BROOKS & DODSON (1965). Since then these ideas have been confirmed in many studies (GULATI et al., 1990, and references therein). Less information is available about the impact of zooplanktivorous urodele amphibians. Early studies with *Ambystoma tigrinum* in shallow Colorado Alpine ponds have shown that this species exploited the available resources in a manner nearly identical to fish (DODSON, 1970; ZARET, 1980). On the other hand, detailed studies about community effects of zooplanktivorous urodeles have shown a weaker impact (MORIN et al., 1983, MORIN, 1987; TAYLOR et al., 1988; STROHMEIER & CROWLEY, 1989). Whereas ZARET (1980) described *Ambystoma* as a "fish in amphibians garments", STROHMEIER & CROWLEY (1989) anticipated a low predation pressure of *Notophthalmus viridescens* on invertebrates compared to foraging fish.

In the Alps, *Triturus alpestris* is the only urodele species inhabiting high altitude water bodies. In Alpine ponds and lakes, *Triturus alpestris* is normally associated with big, planktonic daphniids or diaptomid copepods, whereas, in lakes that contain introduced fish, rotifers and small benthic crustaceans dominate the zooplankton (authors' unpublished observations). In a detailed study we were able to show that daily food consumption of Alpine newts is less than in salmonid fishes (SCHABETSBERGER & JERSABEK, in press).

TABLE I. – Morphometric parameters and abiotic conditions of lakes Großer Feichtauersee and Kleiner Feichtauersee.

	Großer Feichtauersee	Kleiner Feichtauersee
Altitude	1400 m	1390 m
Surface area	11344 m^2	5174 m^2
Volume	30550 m^3	7021 m^3
Max. length	172 m	98 m
Max. depth	11.8 m	4.1 m
Max. surface temperature	19.2 °C	21.2 °C
pH	7.55 - 8.64	7.30 - 8.42
Conductivity (25 °C)	137 - 235 μS	125 - 192 μS

In this study, we present data about zooplankton communities of the two neighboring lakes Großer Feichtauersee (Lake 1) and Kleiner Feichtauersee (Lake 2). Lake 1 contains the European minnow (*Phoxinus phoxinus*) and in Lake 2 Alpine newts are the top predators.

MATERIAL AND METHODS

Lakes 1 and 2 are situated in the North Eastern calcareous Alps of Austria. Both lakes are just 50 m apart from each other and get their water from underground karst springs. Whereas Lake 1 maintained its water level throughout the year, Lake 2 lost over 90 % of its spring water content during summer. In very dry summers Lake 2 can dry out. Apart from this differences in hydrology, abiotic conditions of both lakes were very similar (Tab. I). Both lakes were supersaturated with oxygen during summer. In winter the lakes were covered with a 1.5 to 3 m thick ice-cover, which caused an oxygen depletion down to 50 % saturation directly under the ice. Nevertheless, no anoxic conditions could be found.

Water chemistry was analyzed following standard methods in a professional hydrochemical laboratory (Forschungsstelle Nationalpark Kalkalpen, 4591 Molln, Austria). Zooplankton samples were taken with a Schindler-Patalas plankton trap (5 l) in monthly intervals.

Adult newts were caught by scuba diving, anaesthetized with MS 222 and marked individually (121 males; 89 females) by tattooing with Alcian Blue according to JOLY & MIAUD (1990). Population size was estimated with a multiple mark recapture method (Jolly-Seber method, in KREBS, 1989).

Stomach contents were secured with a stomach flushing technique and preserved in 4 % formaldehyde. Prey items were determined and counted for diet analysis. Stomach contents were divided into 8 prey categories: Amphipoda (*Niphargus* sp.); (micro-) crustaceans (mainly *Daphnia rosea* and *Arctodiaptomus alpinus*); Hemiptera (*Sigara carinata*); terrestrial prey (different Pterygota); Mollusca (*Pisidium* sp. and *Bythinia tentaculata*); Coleoptera larvae (*Agabus solieri* and *Hydroporus palustris*); Trichoptera larvae (*Limnephilus sp.*); skin sloughs. Prey categories were pooled for each sex and sampling date, dried to constant weight at 60°C and weighed to the nearest 10 µg.

The "Index of relative importance" (IRI) was calculated for the different food categories at consecutive sampling occasions (PINKAS et al., 1971):

$$IRI = (\% N + \% W) \times \% O,$$

where:

% N = prey category as percent of total number of ingested prey;
% W = prey category as percent of total weight of ingested prey;
% O = percent of stomachs containing prey category.

Sexually mature minnows were collected in the littoral zone by electro-fishing. They were anaesthetized with a dilute solution of MS 222 and marked with one blue spot ventrocaudal of the anal fin, using the same technique as described for the newts. After the marking procedure, the fish were rinsed in a commercial antiseptic solution (Tetramin) to prevent infection with Fungi or Protozoa.

Population size was estimated with a multiple mark recapture model (Schuhmacher method in KREBS, 1989). In total, 2891 minnows were marked on four different sampling occasions (17.06, 2.07, 19.07, 2.08.1992).

RESULTS

Big crustacean species like the cladoceran *Daphnia rosea* and the calanoid copepod *Arctodiaptomus alpinus* dominate the zooplankton in Lake 2. In addition, benthic species like *Macrocyclops fuscus*, *Megacyclops viridis* and *Eucyclops serrulatus* could be found in the open water. The size (body length) of adult crustaceans ranged from 1.5 to 3 mm.

In contrast, only small rotifers and small developmental stages of cyclopoid copepods occur in the pelagial zone of Lake 1. Cold stenotherm species like *Keratella hiemalis*, *Notholca squamula*, *Polyarthra dolichoptera*, *Synchaeta lakowitziana*, *Anuraeopsis miracleae* and *Filinia hofmanni* are present in the lake throughout the year. Further, the eurytherm species *Synchaeta pectinata*, *Polyarthra remata* and *Ascomorpha ecaudis* colonize the open water. All of these zooplankton species are smaller than 0.5 mm.

There was no evidence that differences in chemistry or hydrology are solely responsible for the differences between the two zooplankton communities. In fact, the deeper Lake 1 would be an ideal habitat for the crustacean species occurring in Lake 2.

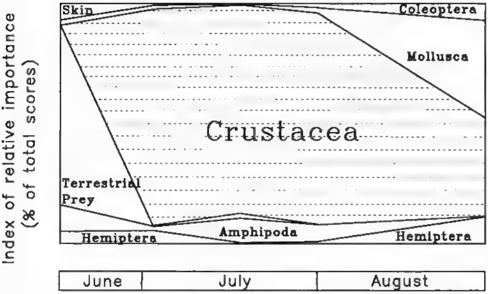

Fig 1. — Temporal changes in the diet of adult *Triturus alpestris*. "Index of relative importance" of different prey categories as percent of total scores.

Total population size of Alpine newts in Lake 2 was estimated to reach 1570 adults (95 % confidence interval: 206-16777) at the beginning of their aquatic period (04.07.1992). No marked animals were caught at the second sampling occasion resulting in poor confidence limits and probably in an overestimation of population size. After 2 weeks (18.07.1992), population size had dropped to a more reliable number of 270 animals (84-1046).

Total population size of sexually mature minnows in Lake 1 was estimated to be 17422 individuals (16638-18570). Confidence limits were narrow, as approximately 13 % of the total population were marked. The abundance of adult Alpine newts was at least ten times less than that of minnows.

Alpine newts did use crustaceans as a major food resource (fig. 1). At the end of July, *Daphnia rosea* constituted more than 98 % of all ingested food organisms. This resulted from an interesting feeding strategy of newts. *Daphnia rosea* reached very high densities in the shadows of rocks. Adult newts struck upwards into these aggregations with their anterior legs up and their mouth open. They probably ingested several individuals with one stroke.

Discussion

In Alpine lakes, calanoid copepods usually produce only resting eggs during summer. The eggs sink to the lake bottom and hatching of nauplii occurs in the next spring (univoltine reproduction). This strategy of reproduction makes these species more vulnerable to predation compared to species producing several generations during one season. Bright red coloration in some high altitude calanoid copepods is another disadvantage when optically oriented predator fish are introduced into the lakes. Daphniids in high altitude water bodies are usually large species and have fewer generations than species in lowland lakes. Although the newts did use crustaceans as a major food resource, their predation pressure seems not to be sufficient to eliminate these populations. Daily food consumption of Alpine newts is less than that of fish of comparable body weight due to lower gastric evacuation rates in newts (SCHABETSBERGER, 1994; SCHABETSBERGER & JERSABEK, in press). Further, the newts are restricted to feeding near the sediment and adults exploit the habitat only during the summer months. Newt larvae also use these crustaceans as prey (SCHABETSBERGER, 1993). The larvae often die under the long ice cover of Alpine water bodies (BRAND & GROSSENBACHER, 1979). If they can survive, low temperatures cause low gastric evacuation rates and a smaller impact on prey communities compared to teleost fishes (SCHABETSBERGER, 1994).

On the other hand, minnows seemed to have eliminated one of their own food resources. All size classes are facultative zooplanktivorous predators (LAZZARO, 1987). There is no plausible explanation for the total absence of big crustaceans in the zooplankton community of Lake 1 other than that of extinction due to predation by fish. Most likely the minnows were introduced into Lake 1 long ago, either for cooking purposes (FROST, 1943), or as bait-fish for salmonids. The Alpine pasture near the lakes have been used for cattle farming for hundreds of years. Minnows were found to survive in lakes where oxygen depletion in winter prevents survival of salmonids. Since the outflow of Lake 1 falls over several cascades, a colonization by anadromous fish is impossible. In other respects, a passive transport of fish eggs in the plumage of water fowl is extremely unlikely.

Total population size of minnows is usually bigger than that of Alpine newts, because the fish have higher fecundity when the lake is suitable for reproduction. Often salmonid fish are introduced in large numbers and compete for the scarce resources in the oligotrophic Alpine lakes. The population size of Alpine newts in high altitude lakes seems to be limited by factors such as high mortality rates during metamorphosis and migration (SCHABETSBERGER & GOLDSCHMID, 1994).

Fish stocking in Alpine lakes causes irreversible changes in zooplankton communities, because the prey species are not adapted to actively foraging fish. Beside these changes in zooplankton, amphibian populations usually disappear shortly after fish introduction, because predatory fish prey heavily on their eggs and larvae (GIACOMA, 1989). In Austria, the introduction of fish into fishless high altitude lakes dates back into the middle ages (PECHLANER, 1966) and is today encouraged by some fishery biologists, as stocking has become easier with the use of helicopters.

The native Arctic charr (*Salvelinus alpinus salvelinus*) has become an endangered species in the Alpine lowland lakes of Austria due to mismanagement and the introduction of North American salmonids as competitors (JAGSCH, 1987). Fishery biologists have argued to introduce Arctic charr into fishless Alpine lakes for conservation of a gene-pool of this endemic subspecies in the Alps (STEINER, 1987). Often other North American charr species or different charr hybrids are introduced instead of Arctic charr, as these fish are more easily available from commercial hatcheries. Since the introduction of fish causes a degradation of these ecosystems, we strongly recommend the protection of fish species by better management in their natural habitats. Although many of these high altitude lakes are situated in existing or planned national parks, Austrian fishery law still allows these stocking activities. The introduction of alien North American charr as well as the degradation of the natural amphibian and zooplankton communities conflicts with the principles of a national park.

Résumé

Les communautés zooplanctoniques de deux lacs karstiques alpins voisins l'un de l'autre, similaires par leurs dimensions et leurs caractéristiques abiotiques, s'avèrent différer beaucoup l'une de l'autre. Dans le premier des deux lacs, le triton alpestre (*Triturus alpestris*) exploite les ressources nutritives pendant l'été, tandis que dans l'autre, un poisson (le vairon européen, *Phoxinus phoxinus*) est le super-prédateur. La communauté zooplanctonique du lac sans poissons se compose de quelques grandes espèces de crustacés, alors que dans l'autre lac les rotifères dominent. Bien que la nourriture des tritons se compose surtout de crustacés, leur pression prédatrice est moindre que celle des poissons. L'effectif de la population des tritons adultes est au moins dix fois inférieur à celui des poissons sexuellement mûrs (1570 tritons contre 17420 vairons).

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Literature cited

Brand, M. & Grossenbacher, K., 1979. – *Untersuchungen zur Entwicklungsgeschwindigkeit der Larven von* Triturus a. alpestris *(Laurenti 1768),* Bufo b. bufo *(Linnaeus 1758) und* Rana t. temporaria *(Linnaeus 1758) aus Populationen verschiedener Höhenstufen in den schweizer Alpen.* Dissertation, Universität Bern: 1-260.

Brooks, J. L. & Dodson, S. I., 1965. – Predation, body size, and composition of plankton. *Science*, **150**: 28-35.

Dodson, S. I., 1970. – Complementary feeding niches sustained by size-selective predation. *Limnol. & Oceanog.*, **15**: 131-137.

Frost, W. E., 1943. – The natural history of the minnow, *Phoxinus phoxinus*. *J. anim. Ecol.*, **12**: 139-162.

Giacoma, C., 1988. – The ecology and distribution of newts in Italy. *Annuar. Ist. Mus. Zool. Univ. Napoli*, **26**: 49-84

GULATI, R. D., LAMMENS, E. H. R. R., MEIJER, M.-L. & VAN DONK, E. (eds.), 1990. — Biomanipulation — tool for water management. Proceedings of an international conference held in Amsterdam, The Netherlands, 8-11 August, 1989. *Developments in Hydrobiology*, Dordrecht, Kluwer Acad. Publishers, **61**: 1-628 (Reprinted from *Hydrobiologia* **200/201**).

HRBÁČEK, J., 1962. — Species composition and the amount of zooplankton in relation to the fish stock. *Rozpr. cesk. Akad. Ved. Rada. Mat. Prir.*, 72: 1-117.

JAGSCH, A., 1987. — Arctic charr in some of the lakes of the eastern Alps (Austria). *Proc. Fourth ISACF Workshop on Arctic Charr, 1986*, Sweden, Institute of Freshwater Research Drottningholm: 64-72.

JOLY, P. & MIAUD, C., 1990. — Tattooing as an individual marking technique in urodeles. *Alytes*, **8**: 11-16.

KREBS, C. J., 1989. — *Ecological methodology*. New York, Harper & Row Publishers: 1-652.

LAZZARO, X., 1987. — A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia*, **146**: 97-167.

MIAUD, C., 1990. — *La dynamique des populations subdivisées: étude comparative chez trois amphibiens urodèles* (Triturus alpestris, T. helveticus *et* T. cristatus). Thèse de Doctorat, Univ. Claude Bernard Lyon I: 1-205.

MORIN, P. J., 1987. — Salamander predation, prey facilitation, and seasonal succession in microcrustacean communities. *In*: W. C. KERFOOT & A. SIH (eds.), *Predation: direct and indirect impacts on aquatic communities*, Hanover, New Hampshire, Univ. Press of New England: 174-188.

MORIN, P. J., WILBUR, H. M. & HARRIS, R. D., 1983. — Salamander predation and the structure of experimental communities: responses of *Notophthalmus* and microcrustacea. *Ecology*, **64**: 1430-1436.

PECHLANER, R., 1966. — Salmonideneinsätze in Hochgebirgsseen und -tümpel der Ostalpen. *Verh. internat. Verein. Limnol.*, **16**: 1182-1191.

PINKAS, L., OLIPHANT, M. S. & IVERSON, I. L. K., 1971. — Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif. Fish Game*, **152**: 1-105.

SCHABETSBERGER, R., 1993. — *Der Bergmolch (*Triturus alpestris, *Laurenti) als Endkonsument in einem alpinen Karstsee (Dreibrüdersee, 1643 m, Totes Gebirge)*. Dissertation, Universität Salzburg: 1-129.

----- 1994. — Gastric evacuation rates of adult and larval Alpine newts (*Triturus alpestris*) under laboratory and field conditions. *Freshwater Biol.*, **31**: 143-151.

SCHABETSBERGER, R. & GOLDSCHMID, A., 1994. — Age structure and survival rate in Alpine newts (*Triturus alpestris*) at high altitude. *Alytes*, **12**: 41-47.

SCHABETSBERGER, R. & JERSABEK, C. D., in press. — Alpine newts (*Triturus alpestris*) as top predators in a high altitude karst lake: daily food consumption and impact on the copepod *Arctodiaptomus alpinus*. *Freshwater Biol.*, in press.

STEINER, V., 1987. — *Die Hochgebirgsseen Tirols aus fischereilicher Sicht. Teil 1. Bestandsaufnahme 1980-1985*. Innsbruck, Studie im Auftrag des Amtes der Tiroler Landesregierung: 1-213.

STROHMEIER, K. L. & CROWLEY, H., 1989. — Effects of red-spotted newts (*Notophthalmus viridescens*) on the densities of invertebrates in a permanent, fish free pond: a one month enclosure experiment. *J. Freshwater Ecol.*, **5**: 53-65.

TAYLOR, B. E., ESTES, R. A., PECHMANN, J. H. K. & SEMLITSCH, R. D., 1988. — Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. *Can. J. Zool.*, **66**: 2191-2198.

ZARET, T. M., 1980. — *Predation and freshwater communities*. New Haven & London, Yale University Press: 1-187.

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